

Weaning in the Norway Rat: Relation Between Suckling and Milk, and Suckling and Independent Ingestion

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We examined in rat pups the relation between the decline of suckling and the emergence of independent ingestion, and the role of milk delivery conditional on nipple attachment in the maintenance of suckling. Fifteen-day-old litters were reared for either 5 or 10 days, and 20-day-old litters for 5 days by either a thelectomized (no nipples), ligated (nipples but no milk), or intact (nipples and milk) dam. Pups' food and water intakes were monitored daily, and their suckling, feeding, and drinking behaviors were videorecorded for 24 hr in the presence of their foster dam (Day 19 or 24) and for 24 hr in the presence of an intact, lactating dam (Day 20 or 25). There were no differences between treatment conditions with respect to either the onset or rate of increase of independent feeding or drinking. Pups reared by a thelectomized dam for 10 days displayed a pronounced, lasting depression of suckling. Twenty-five-day-old pups reared by a ligated dam displayed suckling levels comparable to those of control pups; in the presence of the ligated dam, however, their tendency to attach to a nipple was notably reduced. The implications of the findings for our understanding of the weaning process are discussed.

It has been amply documented that rat pups begin to feed and drink independently around the same time they begin to suckle less (e.g., Babicky, Parizek, Ostadalova, & Kolar, 1973; Babicky, Pavlik, Parizek, Ostadalova, & Kolar, 1972; Henning, 1981; Henning, Chang, & Gisel, 1979; Redman & Sweney, 1976; Thiels, Alberts, & Cramer, 1990). Indeed, weaning frequently is characterized as the developmental period during which suckling and independent feeding co-exist (e.g., Hall & Williams, 1983), and one mode of ingestion gradually replaces, or "substitutes" for the other. The concept of a developmental substitution of suck-

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Received for publication 27 April 1990
Revised for publication 25 July 1990
Accepted at Wiley 3 October 1990

Developmental Psychobiology 24(1):019-038 (1991)
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CCC 0012-1630/91/010019-20\$04.00

ling by independent feeding is reinforced by demonstrations that around the onset of weaning, suckling becomes increasingly controlled by the same physiological and experiential factors that govern food intake (Blass, Beardsley, & Hall, 1979; Blass, Hall, & Teicher, 1979; Cramer & Blass, 1983; Gisel & Henning, 1979; Hall & Rosenblatt, 1977, 1978; Henning et al., 1979; Kenny, Stoloff, Bruno, & Blass, 1979; Lorenz, 1983; Lorenz, Ellis, & Epstein, 1982; Lytle, Moorcroft, & Campbell, 1971; Martin & Alberts, 1979), and by detailed records of the reciprocal shift from exclusive ingestion of milk to exclusive ingestion of solid food in weaning-age rat pups (Babicky, Ostadalova, Parizek, & Kolar, 1971; Babicky, Ostadalova, Parizek, Kolar, & Bibr, 1973; Babicky et al., 1973; Henning et al., 1979; Redman & Sweney, 1976).

However, various lines of research suggest that suckling and independent feeding may not be behavioral substitutes (Allison, 1983), that is, different forms of the same behavior system. First, pharmacologically induced blockade of the serotonin system enhances weaning-age pups' propensity to suckle but has no facilitative effects on their solid food intake (Stoloff & Supinsky, 1985; Williams, Hall, & Rosenblatt, 1980; Williams, Rosenblatt, & Hall, 1979). Second, rat pups continue to suckle well beyond the age at which solid food begins to constitute their primary or only source of nutrition (Cramer, Thiels, & Alberts, 1990; Thiels et al., 1990). The emergence and firm establishment of independent feeding into pups' daily activities thus does not entail contemporaneous abandonment of suckling (see also Pfister, Cramer, & Blass, 1986). Third, weaning-age pups maintain nipple contact despite obtaining little or no milk, whether because of diminished milk supply during late lactation or experimental involution of the dam's nipples (Stoloff & Blass, 1983; Thiels et al., 1990). This resistance to extinction of suckling may be due to a long history of partial reinforcement of nipple attachment, as milk ejections in the rat occur in pulses during continuous attachment to the nipples by the pups (Lincoln, Hill, & Wakerly, 1973; Wakerley & Lincoln, 1971). Alternatively, it may indicate that in weaning-age pups suckling is not maintained primarily by nutritive factors (Cramer & Blass, 1985; Gisel & Henning, 1980; but see Lichtman & Cramer, 1989a), in contrast to independent feeding (Melcer, 1987). In short, there is well-founded reason to suspect that the controls of suckling and independent feeding may have little in common (Drewett, 1978; Hall, 1985; Hall & Williams, 1983), and that the developmental processes that underlie these two behaviors may operate much more independently than their joint timing suggests.

The goals of the present study were to (1) further characterize the relation between the decline of suckling and the emergence of independent ingestion in rat pups, and (2) investigate the role of milk in the maintenance of suckling during weaning. To those ends, we exposed rat pups at various stages during the weaning period to either of three nipple attachment conditions and assessed the effects on pups' inclination to suckle, and to independently feed and drink. The first group of pups was placed with normal, lactating rat dams. Pups in this group experienced nipple attachment and milk in association with one another. A second group of pups was placed with dams whose nipples had been ligated; to maintain growth, these pups received vitamin-enriched cow's milk via gastric intubations administered outside the home cage. This group also experienced nipple attachment and milk, but in dissociation from one another. If milk contingent on suckling is critical for the maintenance of suckling, then pups in this group should exhibit depressed

levels of nipple attachment compared to pups of the first group. A third group of pups was placed with dams whose nipples had been thelectomized (removed); these pups also received vitamin-enriched cow's milk via gastric intubations outside the home cage. Pups in this group experienced milk and other aspects of maternal care, but not the opportunity to attach to a nipple. If the decline of suckling and the emergence of independent feeding are interdependent processes, then pups in this group should commence solid food and water intake significantly earlier than pups continuously provided with the opportunity to suckle (i.e., pups of the first and possibly, second group).

We exposed pups to one of the three treatment conditions either around the onset of weaning (Days 15 through 19), or when weaning was well underway (Days 20 through 24). To assess effects of the differential treatments that may not surface at the younger ages, we exposed some pups to the respective conditions during both treatment periods (i.e., from Day 15 through 24). Behavior differences between the latter two age groups would be suggestive of early treatment effects.

The effects of the different treatment conditions were measured by observing pups' behavior patterns during the final 24 hr of the treatment period, that is, when still housing with either a normal, ligated, or thelectomized dam, and during the first 24 hr after the treatment period when returned to a nipple-intact, lactating dam. Pups' behavior patterns were monitored continuously with the aid of timelapse videography. As detailed elsewhere (Cramer et al., 1990; Thiels et al., 1990), this recording technique permitted capture of undisturbed behavior patterns while avoiding time-based sampling errors. In addition to suckling (i.e., nipple contact with or without attachment and with or without sucking milk, depending on the condition of the caretaker), independent feeding, and independent drinking, we also charted self-grooming and play-fighting. Previous research from our laboratory has shown that independent feeding and drinking emerge embedded in a general transition to behaviors that are performed outside the nest and independent of the caretaker (Thiels et al., 1990). Like feeding and drinking, self-grooming and play-fighting belong to this class of independent behaviors; their inclusion into our present observations permitted us to determine whether alteration of the decline of suckling affects the developmental profile of the entire class of independent behaviors or specifically that of independent ingestion. We also charted the presence in or near the nest of the respective caretakers to take into account possible differences in dams' accessibility to the pups. Finally, to compare onset and rate of increase of solid food and water intake between the three treatment conditions, we measured pups' food and water consumption every 12 hr; to compare growth between conditions, we recorded pups' body weights every 24 hr.

Methods

Subjects

A total of 54 primiparous and multiparous female Sprague-Dawley rats and their litters (432 pups) served in this experiment. The females were outbred from stock originally obtained from Charles River (Portage, MI) and were born in the Animal Behavior Laboratory colony at Indiana University. Impregnated females were housed in standard polypropylene maternity cages (48 × 20 × 26 cm) with

Purina Rat Chow and tap water freely available. Cages were checked daily around 1700 hr, and pups found at that time were considered born on that day (Day 0). Experimental litters were pairwise age-matched, and foster litters were born within ± 24 hr of a pair of experimental litters. Litters were reduced to 8 pups (4 females, 4 males) on Day 3. Experimentation began on the evening of Day 10 for experimental mothers and litters, and on the evening of Day 11 for foster mothers and their litters. The colony rooms were maintained at 24° to 26°C and illuminated from 0700 to 2300 hr. At the start of the experiment proper, experimental litters were established in a room maintained at 23° to 26°C with the same light regimen as the colony rooms. A 25-watt red light bulb illuminated that room during the 8-hr dark period for purposes of videography.

Apparatus

Experimental habitats were specially designed to allow us to (1) assess dams' and pups' food and water intake separately, and (2) monitor animals in each chamber of the habitat from one camera position. The habitats have been described in detail elsewhere (Cramer et al., 1990). Briefly, each habitat consisted of one large nest compartment (27 × 32 × 35.5 cm) and two separate feeding compartments (27 × 16 × 35.5), one for the dam and one for the pups. As illustrated in Figure 1, a small opening (4 × 2.5 cm) at the base of the wall between the nest compartment and pups' feeding compartment permitted passage to pups only, and a notch (16 × 5 cm) at the top of the wall between the nest compartment and the dam's feeding compartment allowed crossing between the two sites to dams only.

The wall between the two feeding compartments and both external wide walls were made of Plexiglas to permit unobstructed view of animals in each chamber of the habitat. The remaining walls and chamber floors were made of aluminum, and the lid of hardware cloth. The pups' feeding compartment was equipped with a food tray covered by an aluminum lid with 5 holes (2.5 cm diameter) to reduce food spillage and a drinking spout. Similarly, the dam's feeding compartment contained an aluminum food tray designed to prevent spillage and a drinking spout. Powdered Purina Rat Chow and tap water were freely available in both feeding compartments during the entire experiment. Wood shavings covered all floors and were replaced every 4 to 7 days. Foster litters were housed in habitats similar in design to those described above, except for slight differences in the size of the respective compartments (nest compartment: 30 × 32 × 35.5 cm; dam's feeding compartment: 24 × 20 × 35.5 cm; pups' feeding compartment: 24 × 12 × 35.5 cm; for details, see Thiels & Alberts, 1985).

Pups' body weights and food intake were measured to the nearest 0.1 g and 0.01 g, respectively, with an analytical balance (Mettler, Type PC 400). Two cameras were used (Panasonic, Model V-1500X and -1550; Cosmocar lenses), attached to a video screen splitter (RCV, Model 1470A) that was connected to a timelapse videocassette recorder (GYR, Model TLC 2001) to videomonitor two habitats simultaneously. The videographic data was coded and analyzed with the aid of a TV monitor (Panasonic, Model 930) and a microcomputer (Radio Shack, TRS-80, Model 4P).

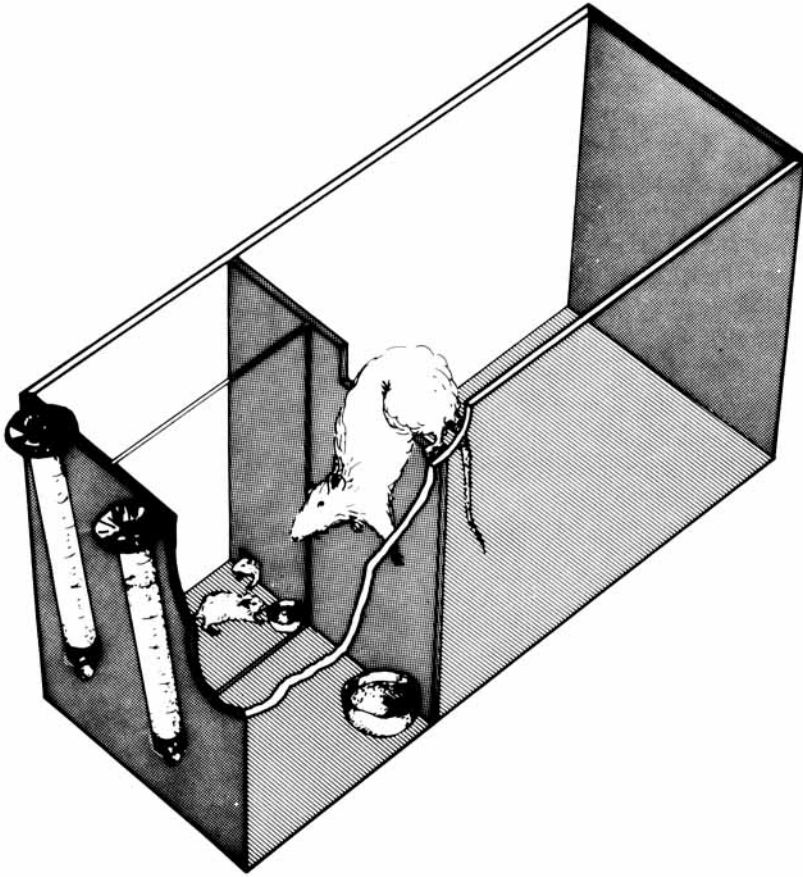


Fig. 1. Illustration of experimental habitat that permitted separate assessment of maternal and pup food and water intake, and easy videography of all compartments due to Plexiglas walls.

Surgical Procedures

Dams whose nipples had been surgically ligated served as caretakers with the behavioral and physiological characteristics of rat mothers (Lynch, 1976), but provided no milk. Dams whose nipples had been surgically removed (i.e., thelectomized) likewise served as caretakers with features typical of rat mothers, but provided neither nipples to attach nor milk. Pups readily attached to the nipples of the ligated dams and contacted the ventral region of the thelectomized dams. Operated females, in turn, readily hovered over the litter, licked the pups, and, in the case of ligated dams, allowed the pups to attach to their nipples.

Dams were ligated when experimental litters were 14 days of age. Around 0800 hr, dams were anesthetized with chloral hydrate (400 mg/kg), a small incision was made at the base of each nipple, the collecting duct ligated with surgical silk (Ethicon Type B, Size 5-0), and the incision sutured closed. The dams were allowed a 5-hr recovery period before reuniting them with their litter in the habitats. Litters rested in an incubator (Isolette, Air-Shields Inc.) maintained at

31°C during the surgery and recovery periods. To determine the success of surgery in blocking milk transfer, ligated females were placed with a 4-hr deprived 7- to 9-day-old litter at midpoint of their foster term, and litter weight change during a 2-hr period was assessed. In each case a weight loss was noted, which suggests that these ligated dams provided no milk. In support of this conclusion, we noted that pups attached to the nipples of those ligated dams never displayed stretch responses, the bodily reflex characteristic for the transfer of milk to the pups (Lincoln et al., 1973).

Dams were thelectomized in the morning following parturition (i.e., Day 1). Around 0800 hr, they were anesthetized with ether, each nipple extruded, clamped at its base with forceps, and the mammae removed with a scalpel. The dams were allowed a 6-hr recovery period before pairing them with 6 to 8 recently nursed 1-day-old pups. Every 8 to 9 hr thereafter, the stimulus pups were replaced with pups of the same age (± 1 day) that had been nursed for at least 24 hr prior to the exchange. This procedure insured that thelectomized dams remained maternal and accommodated to pups of a similar age as experimental pups (Rosenblatt & Lehrman, 1963; Weisner & Sheard, 1933). To minimize the number of females receiving thelectomy, we used each thelectomized dam as foster mother two or three times. They never fostered pups of the same age group twice (see below). Dams were maintained in the maternal state between successive terms, employing the same procedure described above.

Design

During the treatment phase, pups resided with either a control (i.e., unmanipulated) foster mother (CTRL), a ligated foster mother (LIG), or a thelectomized foster mother (THEL). Age and duration of exposure to foster mothers varied within each treatment condition. Pups resided with a foster mother either from the evening of Day 14 through 19 (5 days; Age Group I), the evening of Day 19 through 24 (5 days; Age Group II), or the evening of Day 14 through 24 (10 days; Age Group III). Thus, there were in total 9 subgroups, 3 age groups nested within each of the 3 attachment conditions. During the course of the experiment, it was necessary to delete two CTRL-litters (and their foster mothers and litters) because the mothers failed to nurse the pups, two CTRL-litters because the mothers carried the pups into their feeding compartment on the day of testing, one LIG-litter because the mother failed to enter the nest compartment on the day of testing, and one LIG- and three THEL-litters because of low pup survival (see below). Each of these litters was replaced to obtain complete data of 27 litters, 3 litters per subgroup.

Procedure

Preparation of experimental litters began on the evening of Day 10. The pups were ear-marked, weighed and then distributed between their own mother and a second 10-day-postpartum dam. Half of each litter (2 female and 2 male pups) was returned to its own mother and the other half placed with the second dam whose pups were similarly redistributed between the two mothers. This partial cross-fostering arrangement preserved litter size while altering the number of genetic

Table 1
Milk Intubation Regimen for Pups of the THEL- and LIG-Conditions.

Age	Times/Day ¹	Amount ²	Total Daily Amount ²
Days 15-17	5	5-6%	25-30%
Days 18-19	4	5%	20%
Day 20	3	5%	15%
Day 21	3	4%	12%
Day 22	3	3%	9%
Day 23	3	2%	6%
Day 24	3	1%	3%

¹ Days were considered to begin at 2300 hr; thus, the first intubation of Day 15 was administered at 2300 hr of Day 14, and the last one around 1900 hr of Day 15; the first one of Day 16 at 2300 hr of Day 15, and so on.

² Percent body weight.

siblings per litter (i.e., 2 sets of 4 siblings). It thereby was possible to expose genetic siblings to different foster mothers, and at the same time, "unrelated" pups to the same foster dam during the treatment phase. As a result, we were able to reduce both the number of litters and time required for completion of this experiment.

Mothers and their newly arranged litters were established in experimental habitats where they remained undisturbed except for daily measurement of pups' body weights around 2230 hr. Foster mothers (i.e., control, ligated, or thelectomized dams) and their litters were established in experimental habitats the following evening (i.e., Day 11). Litters were assigned to the various treatment conditions on the evening of Day 14 when foster mothers were placed with litters of Age Groups I and III (CTRL-I, LIG-I, THEL-I, and CTRL-III, LIG-III, THEL-III, respectively). Mothers of the respective experimental litters were paired with the corresponding litters of the foster dams. Daily recordings of pups' food and water intake at 1030 and 2230 hr also began for all 9 groups on the evening of Day 14.

Bodily growth was equalized between treatment conditions by intubating evaporated milk (Carnation) into the stomachs of pups from the LIG- and THEL-Conditions. The evaporated milk was laced with baby vitamins (Poly-Vi-Sol, Mead Johnson; 1 ml/147 ml of milk). Intubation involved carefully passing a cannula (PE-50; Adams Clay) through the pups' oropharynx into the stomach and delivering the appropriate amount of milk from a hand-held syringe to which the cannula was attached. Table 1 shows the intubation regimen, developed in pilot studies. Both the amount and the frequency of milk intubations were reduced as pups grew older, which, together with the use of vitamin-enriched milk served to approximate the diet provided to pups in the LIG- and THEL-Conditions to the natural diet received by control pups.

Control pups received sham intubations with an empty, unattached cannula on the same schedule used for milk intubations. On rare occasions, a pup died during intubation due to inadvertent insertion of the cannula into its lungs. If this occurred on the first day of the intubation regimen, a pup of equal body size and sex from its foster litter was substituted. Replacement pups never served as focal pups (see below). Experimental pups lost during any subsequent intubations were

not replaced; testing was conducted only with litters that consisted of at least 7 pups, 6 of which were from the original experimental litter.

Videomonitoring of Age Group I-litters began on the evening of Day 18. For that purpose, one female and one male pup were marked for recognition on videotape. These "focal" pups were unrelated, and their body weights were representative of those of their siblings. Age Group I-litters were reunited with their own lactating mother on the evening of Day 19, and videomonitoring (12 hr real time = 1 hr videotape time) was continued for an additional 24-hr period. After reunion with their mother (i.e., on Day 20), pups received no further intubations. Because the evening of Day 19 marked the onset of the treatment phase for the Age Group II-litters, we simply transferred the foster dams from the Age Group I-litters to the corresponding Age Group II-litters, while placing the Age Group II-dams with the appropriate foster litters.

Videomonitoring of Age Groups II and III began on the evening of Day 23. Focal pups were marked as described above, with the additional selection criterion that the focal pups of Age Group II were of the opposite sex from their genetic focal sibling videotaped on Days 19 and 20. Monitoring of Age Group II- and III-pups under uniform treatment conditions (i.e., with their own lactating mother) commenced on the evening of Day 24. As before, pups no longer received milk intubations during the 24-hr observation period with a lactating dam.

Data Analysis

Videographic Data

To quantify the pups' behavior patterns, we used a slightly modified version of the transcription procedure described by Thiels et al. (1990). Briefly, for each focal pup, each day's video record (about 23.1 hr real time) was divided into successive 20-sec segments of real time (1.55 sec of videotape time); these segments were sampled for one of the following "target" behaviors:

(1) **Suckling/nipple attachment or contact:** The focal pup is visibly attached to a nipple, or lying underneath the mother with its snout buried in her nipple region; the pup's orientation, posture, and, when sucking on a nipple of an intact dam, occasional stretch responses helped to distinguish nipple attachment from mere huddling with the mother. Pups residing with a thelectomized dam obviously could not attach to nipples; they were considered to engage in "suckling" behavior, that is, nipple contact when they positioned themselves in relation to the dam's ventrum in a manner characteristic for suckling.

(2) **Independent feeding:** The focal pup has its snout in the food tray; food handling and/or chewing motions were sometimes discernible.

(3) **Independent drinking:** The focal pup's mouth is in contact with the tip of the water spout; licking motions were often discernible.

(4) **Self-grooming:** The focal pup licks or scratches itself, or moves its forepaws back and forth along its cheeks and/or around its snout.

(5) **Play-fighting:** The focal pup wrestles with a littermate, lying on top or underneath the other pup and is engaged in a rapid exchange of forepaw strikes with the other pup's face; the vividness of pups' movements helped to distinguish play-fighting from social grooming.

(6) **Other activities:** The focal pup engages in none of the above behaviors (i.e., default behavior category).

If a focal pup engaged in more than one of these behaviors during a 20-sec segment, the temporally dominant behavior was assigned to that segment. Sampling of the video records was conducted by a well-trained observer who consistently maintained a high intrarater reliability throughout data transcription (percent overlap between repeated viewings of approximately 2080 20-sec segments, or 11.7 hr real time varied between 88 and 93%). A second, well-trained observer (95 to 98% overlap between repeated viewings of 2080 20-sec segments) sampled video records for the following behaviors of the dams: (1) nursing, or nursing-like posture, in the case of ligated and thelectomized dams, (2) residing in the common nest compartment, but not nursing, and (3) residing in the private feeding chamber. The transcribed data from the dams were used both to identify possible differences between dams of the various treatment groups (see below) and to assess inter-observer reliability. To evaluate inter-observer reliability, we determined for each record the percentage of 20-sec segments during which the pup observer noted nipple attachment or contact, and the dam observer noted behaviors other than nursing. Because this dam-pup behavior combination presents an impossible event, the resulting index indicates inter-rater *disagreement*. The inter-rater disagreement never exceeded 2% of the segments for any of the records.

The transcribed data provided the basis to compute the percent daily time that focal pups allocated to each of the 7 target behaviors while residing with (a) their foster mother (i.e., CTRL-, LIG-, or THEL-dam; Day 19 or 24), and (b) their own lactating mother (Day 20 or 25). Daily behavior profiles for the corresponding dams were created similarly.

Intake Data

In accord with previous studies from our laboratory (Thiels & Alberts, 1985; Thiels et al., 1990), we designated the first occasion on which a litter consumed at least 1.0 g of chow or 2.0 ml of water as the onset of independent feeding or drinking, respectively. We adjusted daily food and water intake measurements relative to body weight to take into account the changes in demand as the pups grow. To that end, we determined for each litter and day the total food and water intake and litter weight and computed intake per pup as a percentage of average body weight.

Group Comparisons

We assessed the effect of treatment condition (CTRL vs. LIG vs. THEL) on growth by comparing focal pups' body weights before and during housing with a foster dam. We used a $3 \times 4 \times 6$ ANOVA (Treatment Condition \times Age \times Subjects) for Age Groups I and III, and a $3 \times 9 \times 6$ ANOVA for Age Group II to compare body weights before the different treatments, and a $3 \times 5 \times 6$ ANOVA (Age Groups I and II) or $3 \times 10 \times 6$ ANOVA (Age Group III) to compare body weights during the different treatments.

To assess the effect of treatment condition on onset of food and water intake, the data of Age Groups I and III within each treatment condition were combined.

Such data pooling was justified because the two age groups were treated identically within each condition until after food and water intake had emerged. The resulting data sets were analyzed statistically with one-way ANOVAs.

Despite cross fostering and selecting only unrelated pups as focal pups for a given treatment condition, the within-litter variability of the pups' behavior tended to be lower than the between-litter variability. For purposes of statistical analysis, we therefore combined the data of each pair of focal pups from the same litter and computed one average behavior profile per litter. We assessed the effect of treatment condition on time allocation to suckling (i.e., nipple attachment or contact), and independent feeding and drinking combined with the aid of Kruskal-Wallis tests (Hollander & Wolfe, 1973). Kruskal-Wallis tests also were used to determine the effect of treatment condition on daily food and water intake and to compare the amount of time that foster dams/mothers spent in the nest compartment (nursing or not nursing).

Results

Overview

Residing with either a ligated or a thelectomized dam and being maintained on artificial milk feeds had no detrimental effects on pups' growth. To the contrary, THEL-pups exhibited slightly greater weight gains than CTRL-pups. The intubation regimen therefore appears to have been adequate to support normal growth. Similarly, residing with a ligated or a thelectomized dam generally had no effects on pups' behavior patterns, except for their inclination to contact/attach to a nipple, and the alterations in suckling behavior rapidly disappeared upon reunion with their own lactating mother. Only pups that resided with a thelectomized dam from Day 15 through 24 exhibited lasting changes in suckling behavior: in contrast to pups reared by control foster dams, the Group III/THEL-pups engaged only briefly and infrequently in suckling bouts during the entire 24-hr observation period with their own mother on Day 25, even though each of the pups attached to its mother's nipples at least once within the first 60 min after reunion. The different trends in pups' suckling behavior could not be attributed to differences in the dams' presence in or near the nest, as the amount of time dams spent in the common nest compartment did not vary between conditions in any of the age groups. Finally, residing with either a ligated or a thelectomized dam had no effect on the initiation of either food or water intake, $F(2,15) = 2.67$, $p > .1$ and $F(2,15) = 1.24$, $p > .3$, respectively. On average, pups began to feed independently on Day 18 and drink on Day 19. Daily food and water intakes were transiently elevated in THEL-compared to CTRL-pups; however, these differences were very slight and often confined to isolated days. A detailed report of these results is presented below.

Age Group I (Foster Treatment from Day 15 Through 19)

There were no systematic differences between conditions in focal pups' body weight before the treatment phase, $F(2,15) = 3.14$, $p > .05$, although THEL-pups generally were slightly heavier than either LIG- or CTRL-pups¹. On the evening

Table 2.

Ranges of the Percent of Daily Time Individual Focal Pups Engaged in Each of the Target Behaviors on Day 19 and Day 20 for THEL-, LIG-, and CTRL-Conditions of Group I.

	DAY 19				
	Suckling ¹	Feeding	Drinking	Grooming	Play-fighting
THEL	0.2–9.7%	5.2–9.1%	0.3–1.1%	3.4–6.4%	1.0–1.9%
LIG	26.8–61.3%	4.2–7.2%	0.2–0.9%	1.4–5.2%	0.6–2.3%
CTRL	34.8–42.4%	3.1–6.0%	0.3–1.1%	1.1–3.6%	0.6–1.3%
	DAY 20				
	Suckling	Feeding	Drinking	Grooming	Play-fighting
THEL	19.6–47.5%	5.1–7.0%	0.4–1.1%	2.4–4.6%	2.0–2.6%
LIG	27.5–46.9%	5.4–7.9%	0.4–1.4%	1.3–4.0%	1.3–2.3%
CTRL	24.8–30.3%	5.5–8.3%	0.6–1.6%	2.2–3.7%	1.0–2.8%

¹ Nipple contact with or without attachment and with or without sucking milk, depending on treatment condition. See text for further explanations.

of Day 14, THEL-pups weighed, on average (\pm SD), 35.3 ± 2.7 g, LIG-pups 32.7 ± 2.4 g, and CTRL-pups 31.7 ± 3.1 g. Initial differences in body weight increased during the treatment phase, and by the end of the treatment phase THEL-pups were significantly heavier than pups from either of the other two conditions. Mean (\pm SD) values on the evening of Day 19 were 48.6 ± 3.7 g, 43.2 ± 3.3 g, and 41.4 ± 3.4 g, respectively; $F(10,75) = 2.22$, $p < 0.05$.

Treatment condition significantly affected the relative amount of time pups spent attached to or in contact with a nipple on Day 19, when pups were still residing with the foster dams, $H[3(3, 3, 3)] = 5.60$, $p = .05$. Pups in the THEL-Condition rarely adopted a suckling-like posture, whereas pups in both remaining groups spent approximately one-third of their day in this behavior. In contrast to the differences in nipple-oriented behavior, the amount of time focal pups allocated to feeding and drinking did not systematically vary between the three conditions, $H[3(3, 3, 3)] = 4.62$, $p > .1$. Analyses of pups' solid food and water intake, relative to body weight, similarly did not reveal significant differences between conditions, $H[3(3, 3, 3)] = 4.27$, $p > .1$ and $H < 1$, respectively. Finally, treatment condition did not appear to systematically affect pups' time allocation to either self-grooming or play-fighting on Day 19. Table 2 shows for each of the three conditions range values of the time allocation to each of the target behaviors.

When pups were reunited with their own lactating mother on Day 20, THEL-pups quickly resumed suckling levels indistinguishable from those of pups in the LIG- and CTRL-Conditions, $H < 1$. There were no reliable differences between conditions in the amount of time focal pups engaged in feeding and drinking on Day 20, ($H < 1$). These findings are illustrated in Panel A of Figure 2, which depicts group medians of the percentage time focal pups allocated to suckling, plotted against the percentage time they spent feeding and drinking. The tight clustering of the three symbols in Panel A reflects the similar patterns of both suckling and independent ingestion among the three treatment conditions. In agreement with

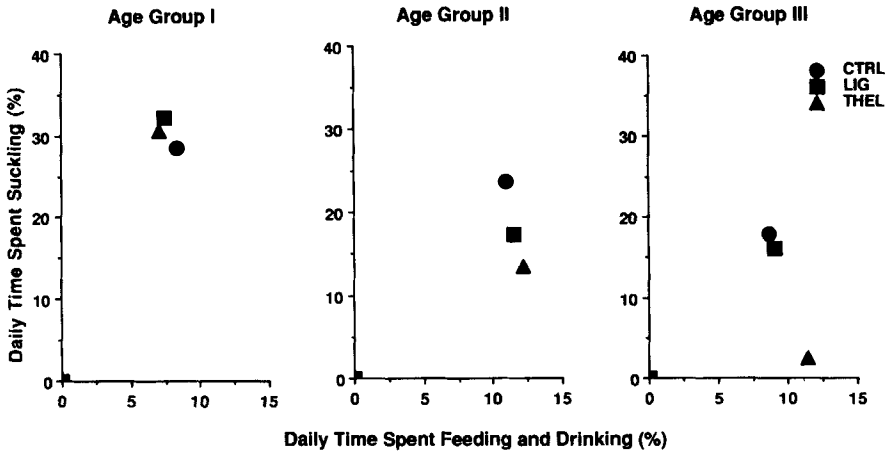


Fig. 2. Median values of the percent of daily time individual focal pups allocated to suckling (Y-axis) and to independent ingestion (X-axis) during testing with a lactating dam for the THEL- (triangles), LIG- (diamonds), and CTRL- (circles) Conditions. The left panel displays the data for Age Group I, the middle panel for Age Group II, and the right panel for Age Group III. See text for further explanations.

the temporal measurement, pups’ relative food and water consumption on Day 20 did not differ significantly between conditions, $H [3 (3, 3, 3)] = 1.16, p > 0.10$ and $H [3 (3, 3, 3)] = 1.87, p > 0.1$, respectively. As shown in the bottom panel of Table 2, time allocation to grooming and play-fighting also was comparable between conditions on Day 20.

Analysis of the caretakers’ daily behavior pattern revealed that the time dams spent in the common nest compartment did not systematically differ between either the set of foster dams on Day 19, $H [3 (3, 3, 3)] = 2.76, p > 0.1$, or the set of lactating dams on Day 20, $H [3 (3, 3, 3)] = 3.69, p > 0.1$. Overall, the percent of daily time that dams were accessible to the pups ranged between 56.4 and 85.3% on Day 19, and between 22.8 and 69.1% on Day 20.

Age Group II (Foster Treatment from Day 20 Through 24)

There were no differences between conditions in focal pups’ body weight either before or during the treatment phase, both $F_s < 1$. Mean (\pm SD) body weights on the evening of Day 19 were 42.3 ± 4.9 g, 44.7 ± 3.0 g, and 40.5 ± 1.6 g in the THEL-, LIG-, and CTRL-groups, respectively, and on the evening of Day 24, the corresponding body weight values were 64.5 ± 6.5 g, 65.8 ± 4.8 g, and 63.6 ± 2.9 g, respectively.

In contrast to the results of the younger age group, both LIG-pups and THEL-pups of Age Group II spent significantly less time attached to/in contact with a nipple while residing with their respective foster dams than did CTRL-pups. There was no overlap between the three conditions in pups’ nipple attachment/contact time on Day 24. Similar to the younger age group, treatment condition had no systematic effect on pups’ time allocation to feeding and drinking, $H [3 (3, 3, 3)] = 2.40, p > .1$. However, both solid food and water intake, relative to body

Table 3.

Ranges of the Percent of Daily Time Individual Focal Pups Engaged in Each of the Target Behaviors on Day 24 and Day 25 for THEL-, LIG-, and CTRL-Conditions of Group II.

	DAY 24				
	Suckling ¹	Feeding	Drinking	Grooming	Play-fighting
THEL	0.0–0.0%	9.6–13.0%	1.6–2.6%	2.7–7.6%	1.1–2.5%
LIG	2.6–14.8%	5.3–13.0%	1.1–2.5%	4.0–6.5%	1.2–3.5%
CTRL	18.2–22.5%	8.3–10.2%	0.8–1.8%	2.9–6.1%	0.6–1.3%
	DAY 25				
	Suckling	Feeding	Drinking	Grooming	Play-fighting
THEL	7.2–21.0%	7.2–10.8%	1.9–2.6%	3.4–7.9%	2.1–3.8%
LIG	4.7–19.0%	5.5–12.7%	1.2–5.5%	4.3–8.9%	2.1–5.5%
CTRL	17.0–27.0%	9.2– 9.9%	1.3–1.9%	4.0–4.8%	1.9–3.2%

¹ Nipple contact with or without attachment and with or without sucking milk, depending on treatment condition. See text for further explanations.

weight, varied reliably between conditions on Day 24, $H [3 (3, 3, 3)] = 5.96$, $p < .05$, and $H [3 (3, 3, 3)] = 5.42$, $p = .07$. On that day, both THEL- and LIG-pups tended to consume more food and water than did CTRL-pups. Table 3 shows for each of the three conditions in Age Group II range values of the time allocation to each of the target behaviors based on individual focal pups' data for both observation days. As can be seen in the top panel, self-grooming and play-fighting were displayed at comparable levels in the three suckling conditions on Day 24.

Despite the pronounced differences in nipple attachment/contact during the treatment phase, the relative amount of time spent suckling on Day 25, when pups were reunited with their own lactating mother, was comparable in the three conditions, $H [3 (3, 3, 3)] = 3.29$, $p > .1$. This is illustrated in Panel B of Figure 2, which also shows group medians of the percent of time that focal pups spent feeding and drinking. The near perfect vertical alignment of data points in Panel B represents the equivalence of feeding and drinking in the three conditions. The slight scatter across conditions in relation to the graph's suckling axis does not reflect systematic differences. Neither time allocation to feeding and drinking nor amount of food and water consumed varied reliably between the three conditions on Day 25, feeding and drinking time: $H < 1$, food intake $H [3 (3, 3, 3)] = 1.16$, $p > .1$, and water intake: $H < 1$. As detailed in the bottom panel of Table 3, time spent self-grooming and play-fighting similarly did not differ between conditions on that day.

The differences in nipple-oriented behavior on Day 24 could not be explained on the basis of the foster dams' availability to the pups; the percentage time that foster dams resided in the common nest compartment did not vary systematically between the three conditions and ranged between 56.8 and 86.0%, $H [3 (3, 3, 3)] = 3.82$, $p > .1$. Pups' own mothers also did not differ significantly with respect to the amount of time spent in the common nest compartment on Day 25, depending on the prior history of attachment to the nipple of the pups, (Range = 41.4 to 77.1%), $H [3 (3, 3, 3)] = 1.69$, $p > .1$.

Table 4.

Ranges of the Percent of Daily Time Individual Focal Pups Engaged in Each of the Target Behaviors on Day 24 and Day 25 for THEL-, LIG-, and CTRL-Conditions of Group III.

	DAY 24				
	Suckling ¹	Feeding	Drinking	Grooming	Play-fighting
THEL	0.0–1.0%	8.4–12.6%	1.6–2.2%	3.9–8.5%	1.9–3.3%
LIG	2.8–18.9%	6.0–11.2%	1.4–2.0%	2.6–6.4%	2.0–3.9%
CTRL	10.5–20.1%	6.0–11.4%	0.6–2.3%	2.6–5.0%	1.6–3.4%
	DAY 25				
	Suckling	Feeding	Drinking	Grooming	Play-fighting
THEL	0.0–3.8 %	8.2–11.4%	1.6–2.2%	4.1–7.9%	2.1–3.9%
LIG	6.5–26.5%	6.3–9.2 %	1.3–1.7%	3.3–5.5%	1.8–4.1%
CTRL	14.2–25.3%	7.2–9.5 %	1.1–1.8%	2.6–6.5%	1.9–3.3%

¹ Nipple contact with or without attachment and with or without sucking milk, depending on treatment condition. See text for further explanations.

Age Group III (Foster Dam from Day 15 Through Day 24)

Focal pups' body weight did not differ significantly between conditions either before or during the treatment phase, both $F_s < 1$. However, THEL-pups gained weight somewhat more rapidly than either LIG- or CTRL-pups during the treatment phase, as indicated by a significant Treatment Condition \times Age Group interaction, $F(20,150) = 2.16, p < .01$. Mean (\pm SD) body weights on the evening of Day 15 were 30.8 ± 2.1 g, 32.4 ± 2.4 g, and 30.2 ± 2.5 g in the THEL-, LIG-, and CTRL-groups, respectively; on the evening of Day 24, the corresponding body weight values were 65.3 ± 3.4 g, 63.4 ± 3.2 g, and 62.4 ± 5.2 g, respectively.

Similar to the pattern noted in Age Group II, type of foster dam significantly influenced pups' inclination to contact/attach to a nipple on Day 24, $H [3 (3, 3, 3)] = 5.96, p < .05$. Whereas THEL-pups rarely adopted a suckling-like posture on Day 24, LIG- and CTRL-pups spent approximately 10 to 15% of their time attached to a nipple. Time allocation to feeding and drinking did not differ systematically between the three conditions, $H [3 (3, 3, 3)] = 2.40, p > .1$, as did not relative food and water intake on that day, $H [3 (3, 3, 3)] = 1.16, p > 0.10$, and $H [3 (3, 3, 3)] = 1.69, p > 0.10$, respectively. There also appeared to be no effect of treatment condition on pups' tendency to self-groom or to play-fight, as can be seen in the top panel of Table 4 which shows for each of the three conditions in Age Group III range values of the time allocation to each target behavior, based on individual focal pups' data, for both observation days.

Panel C of Figure 2 shows that upon reunion with their lactating mothers on Day 25, LIG-pups rapidly resumed levels of suckling comparable to those of CTRL-pups, whereas THEL-pups continued to display extremely low levels of suckling behavior. Although there was no overlap in suckling time between THEL-pups and pups of either of the remaining conditions, statistical analysis revealed that the overall effect of treatment condition on the inclination to suckle on Day 25 was only marginally significant, $H [3 (3, 3, 3)] = 5.42, p = .07$. THEL-pups

spent slightly, but reliably more time feeding and drinking than did pups in either of the remaining conditions on Day 25, $H [3 (3, 3, 3)] = 5.60, p = .05$. That is, the THEL-symbol in Panel C of Figure 2 representing time spent feeding is skewed significantly to the right. The values shown in the lower panel of Table 4 clarify this apparent acceleration in independent ingestion. There was substantial overlap between conditions in time allocated to feeding and drinking, and a significant effect due to treatment condition emerges only when the times allocated to feeding and drinking are combined. Moreover, neither relative food nor relative water intake varied systematically between conditions on that day, both $H_s [3, (3, 3, 3)] = 3.82, p > .1$. Finally, the percent of time that pups engaged in self-grooming and play-fighting were comparable between conditions (see lower panel of Table 4).

The observed differences in suckling behavior between conditions could not be attributed to the behavior of the caretakers. There were no systematic differences between either foster or lactating dams in the percent of daily time they spent in the common nest compartment. On Day 24, the respective values varied between 50.6 and 80.8%, $H [3 (3, 3, 3)] = 1.69, p > .1$, and on Day 25, the values ranged between 45.4 and 82.8%, $H [3 (3, 3, 3)] = 1.69, p > .1$.

Discussion

The present experiment addressed two fundamental issues concerning the weaning process in rat pups, namely: (1) the relation between the decline in suckling and the emergence of independent ingestion, and (2) the role of milk in the maintenance of suckling. The implications of our findings with regard to each of these issues are discussed below.

Relation Between Decline in Suckling and Emergence of Independent Ingestion

To elucidate this issue, we manipulated pups' opportunity to suckle while monitoring their independent feeding and drinking patterns. Beginning on Day 15 postpartum, we found that artificially-fed pups that resided with a thelectomized foster mother (no nipples to attach to and suck on), initiated solid food and water intake no earlier than pups that had uninterrupted suckling opportunity. Moreover, once independent ingestion had been initiated, pups without access to maternal nipples generally consumed daily amounts of food and water comparable to those of pups with access to nipples. The amounts of daily time they engaged in the respective ingestive behaviors, as well as other independent behaviors that have been shown to co-emerge with independent ingestion (Thiels et al., 1990) also were comparable to those of normally-reared pups. Furthermore, artificially-fed pups that resided with a ligated foster dam and thus had only "dry" nipples to attach to, began to feed and drink around the same age as pups with continuous nutritive suckling opportunities, and the development of independent behaviors, including independent ingestion, did not appreciably differ between the two rearing conditions despite notable differences in nipple attachment after Day 20. We therefore conclude that in the absence of noticeable alteration in pups' nutritive condition, neither advanced termination nor accelerated decline of suckling affect the age at

which rat pups first begin to ingest solid food and water, or markedly alter the rate at which pups incorporate these ingesta into their diet.

Pfister et al. (1986) developed a rearing preparation that delays termination of suckling. They noticed that pups suckling until 70 days of age or more nevertheless begin to chew food pellets around the same age as normally-reared pups (Pfister and Cramer, personal communication, 1987). Although precise measurement of food and water intake of these extended sucklers is still needed, this observation by Pfister et al. suggests that delay of the termination of suckling does not affect the onset and rate of transition to nutritive independence. Lack of dependence between suckling and independent ingestion also is illustrated by the finding of normal feeding and drinking patterns by weaning-age pups that were reared artificially, that is, without any opportunity to contact, attach to, or suck on a nipple since birth (Hall, 1975). There thus appears to be strong evidence that the developmental contiguity between the decline of suckling and the appearance of independent ingestion (Thiels et al., 1990) reflects a coincidence rather than a close, functional linkage between these two processes.

This conclusion does not imply that the decline of suckling never plays a role in the emergence of independent feeding, or vice versa. When pups suckle less and their milk intake diminishes, they will be forced to satisfy their nutritive needs with foods selected from the environment. We demonstrated previously that reduced access to maternal milk without compensatory artificial nutritive loads significantly advances the onset of independent food and water intake and accelerates the rate of transition to these alternate sources of nutritive energy (Thiels & Alberts, 1985). Conversely, consumption of solid food reduces pups' level of nutritive deprivation and thereby removes a probable stimulus for nipple attachment in weaning-age pups. Administration of nutritive loads prior to a suckling test has been shown to notably reduce the latency as well as the duration of nipple attachment by pups 2 weeks of age or older (Brake, Sager, Sullivan, & Hofer, 1982; Gisel & Henning, 1979, 1980; Hall, Cramer, & Blass, 1975, 1977; Henning et al., 1979). Initiation of solid food intake might contribute to the decline of suckling also by enabling pups to bypass their mother's milk under certain circumstances. Alberts and associates demonstrated that weaning-age pups express a flavor aversion acquired during suckling only after they had the opportunity to ingest solid food (Alberts & Gubernick, 1984; Martin & Alberts, 1979; but see also Melcer, Alberts, & Gubernick, 1985). Finally, experience with solid food might set the stage for pups to express sensitivity to the high response requirement of nutritive intake from the nipple, and accordingly to reduce suckling levels. The intermittent nature of milk ejection in the rat (Lincoln et al., 1973) makes suckling a rather inefficient mode of food procurement, especially when solid food is available at low procurement cost in the environment. In short, the decline of suckling may serve as a catalyst in the transition to solid food, as may the initiation of solid food intake in the abandonment of suckling. However, the decline of suckling per se appears to be neither necessary nor sufficient for the emergence of independent feeding.

Role of Milk in the Maintenance of Suckling

To elucidate this issue we manipulated pups' opportunity to receive milk contingent upon nipple attachment and monitored its effect on the animals' inclina-

tion to suckle. We found that artificially-fed pups that were housed with a ligated dam between Days 15 and 19 and thus experienced a negative contingency between nipple attachment and milk delivery during that time exhibited levels of nipple attachment comparable to those of pups that uninterruptedly experienced a positive contingency between the two events. Moreover, the former group of pups showed no change in the tendency to attach to a nipple upon re-establishment of a positive contingency between nipple attachment and milk delivery. These findings suggest that prior to Day 20 nipple attachment appears to occur independent of contingent milk delivery. This conclusion is strengthened by our observation of comparable suckling levels between pups that resided with a ligated dam from Day 15 to Day 24 and pups reared under similar conditions from Day 20 to 24. If pups did learn about the dissociation of nipple attachment and milk delivery prior to Day 20, we would expect such learning to be reflected in lower suckling levels in the former compared to the latter group of pups.

In disagreement with our conclusion, Kenny et al. (1979) found that pups as young as 17 days of age display a pronounced preference for milk-providing nipples over "dry" nipples in a two-choice discrimination task. The discrepancy between the findings of Kenny et al. and ours may be due to the fact that, in contrast to our test situation, Kenny et al.'s subjects were severely milk-deprived and presented with a choice between nipple types. Under these special circumstances, then, milk contingent on nipple attachment appears to be able to support higher levels of attachment to the nipple than do "dry" nipples alone, even prior to Day 20.

Our results from the two older age groups indicate that after Day 20 pups begin to be sensitive to the relation between nipple attachment and milk delivery. Twenty-four-day-old pups that resided with a ligated dam spent significantly less time attached to the nipple than did control pups that were housed with a lactating dam, or themselves after being returned to their own lactating mother the next day. This outcome suggests that around the time maternal milk stores begin to recede (Thiels, Cramer, & Alberts, 1988), pups begin to alter their suckling tendency depending on the amount of milk extractable from the nipple. Furthermore, this outcome provides support for the idea that the progressive reduction of milk availability that ensues during late lactation (Thiels et al., 1988) plays an instrumental role in the eventual disappearance of suckling. Lichtman and Cramer (1989a) compared a variety of factors, including nutritive deprivation, social stimulation by younger pups, daily suckling frequency, and milk delivery during nipple attachment, in their ability to delay the termination of suckling. They found milk delivery during nipple attachment to be the most crucial variable and interpreted their findings to indicate that learning about the diminution of milk associated with suckling was one of the primary mechanisms that underlies the disappearance of suckling (Lichtman & Cramer, 1989a).

Role of Nipple Attachment in the Maintenance of Suckling

A noteworthy finding in the present study was that pups that resided with a thelectomized dam from Day 15 through Day 24 displayed significantly lower levels of suckling when returned to a lactating dam than did pups that housed with either a ligated or a lactating dam during this period. Because pups reared by a ligated dam continued to experience the perioral and kinesthetic stimuli associated with suckling, the difference in suckling behavior between the THEL- and the LIG-

Conditions suggests that the decline of suckling would proceed faster if pups were not repeatedly exposed to these aspects of the suckling stimulus complex. Furthermore, it appears that an extended period of no nipple contact is necessary to cause such accelerated termination of suckling, for we did not observe comparably depressed suckling levels in pups that resided with a thelectomized dam for only 5 days, beginning either on Day 15 or Day 20. The mechanism(s) by which those kinesthetic/perioral stimuli maintain suckling are unclear. Because under normal circumstances these stimuli are paired reliably with milk and elevation in body temperature (Leon, Croskerry, & Smith, 1978), both of which are rewarding, they may acquire secondary rewarding (i.e., response maintaining) properties by means of associative learning (Cramer & Blass, 1985; Stoloff, Kenny, Blass, & Hall, 1980). In any event, our findings indicate that some aspects of the act of suckling promote the extinction of that behavior (e.g., the diminishing milk returns), whereas others aid its preservation in pups' behavioral repertoire (e.g., the perioral stimulation of nipple attachment).

In accord with our results, Williams et al. (1980) found that 20- and 25-day-old pups that lived without a caretaker for 5 days spent the same amount of time attached to (dry) nipples of an anesthetized dam as same-aged normally-reared pups. In contrast, 25-day-old pups that lived without a caretaker for 10 days, beginning on Day 15, displayed significantly depressed levels of nipple attachment during subsequent testing (Williams et al., 1980). Together, the findings of Williams et al. and the present ones indicate that (1) suckling is not readily eliminated from pups' behavioral repertoire, and (2) the duration of the period of no nipple contact plays a more critical role in the disappearance of suckling behavior than the age at which pups experience no nipple contact. Lichtman and Cramer (1989b) reached a similar conclusion regarding the relative importance of pups' recent suckling history vs. age in determining their propensity to suckle (but see Williams et al., 1980). The two variables clearly interact because at very young ages (i.e., less than 5 days of age), 12 to 48 hr of no suckling experience are sufficient to severely impede suckling behavior (Dollinger, Holloway, & Dennenberg, 1978; Stoloff et al., 1980).

In summary, the decline of suckling and the emergence of independent ingestion (and other independent behaviors) are not inextricably linked. Milk does not play a key role in the maintenance of nipple attachment until relatively late during weaning. Then, however, progressive diminution of milk yield from the nipple may serve to promote the disappearance of suckling via such a mechanism as learned extinction. Although less important than contingent milk delivery, the perioral and/or kinesthetic stimuli associated with suckling also appear to contribute to the maintenance of that behavior, and repeated exposure to them notably protracts its permanent disappearance.

Notes

¹ Because thelectomized dams served as foster mother twice with only 6 to 8 days between successive foster terms, all THEL-litters were born during the same 2-month period. For unknown reasons, litters born in the colony around that time were unusually heavy. As a result the starting weights of the THEL-pups were slightly heavier than those of pups from either of the remaining conditions.

This work was supported by a grant from the National Institute of Mental Health (#MH-28355) to J.R.A. and an Indiana University Predoctoral Research Fellowship to E.T. The authors wish to thank Dr. C. P. Cramer for critical discussions and continuous encouragement for the studies reported here, Curt Matlock for assistance with programming, and Allen Fear for assistance in data collection. The programs used for computer-generated timesampling and data analysis are available from Dr. C. P. Cramer on request. E.T. now is at the Institut de Biologie Théorique, 10 rue Boguel, 49100 Angers Cédex, France.

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